A peer-reviewed open-access journal
NeoBiota
Advancing research on alien species and biological invasions

NeoBiota 95: 267–278 (2024)
DOI: 10.3897/neobiota.95.126656

Research Article

Comparing the ecological consequences of globally invasive fishes versus their F1 hybrids in recreational fisheries

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Abstract

Recreational angling is a major introduction pathway for non-native fish into freshwaters, where multiple non-native fishes are often released into waterbodies to diversify the angling opportunities. When these non-native fishes are taxonomically similar, then there is concern that their hybridisation will result in F1 generations comprising of novel phenotypes that outperform their parental species, resulting in the impacts of these ecological engineering species being accelerated. Across two water temperatures (18 °C, 26 °C), comparative functional response analyses (CFR) quantified the consumption patterns of the globally invasive freshwater fish common carp *Cyprinus carpio* and goldfish *Carassius auratus*, plus their F1 hybrids, before testing differences in their specific growth rates (SGRs). In CFRs, carp consumed significantly more prey at 18 °C than the other fishes, and with no differences between any of the fishes at 26 °C. SGRs also did not differ substantially between the fishes at either temperature. These results suggest that hybridisation between the high impacting parental species did not produce novel phenotypes of high ecological performance that could accelerate their ecological impacts in invaded ecosystems. Accordingly, the ecological risks of their use in recreational angling remain an issue that is primarily associated with the parent populations, and this can be reflected in their invasion management.

Key words: Common carp, comparative functional response, goldfish, heterosis

OPEN ACCESS

Academic editor: Emili García-Berthou
Received: 1 May 2024
Accepted: 10 September 2024
Published: 14 October 2024

Citation: Tarkan AS, Kurtul I, Britton JR (2024) Comparing the ecological consequences of globally invasive fishes versus their F1 hybrids in recreational fisheries. NeoBiota 95: 267–278. https://doi.org/10.3897/neobiota.95.126656

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Introduction

Recreational angling remains an important introduction pathway for non-native freshwater fishes, where the aims of introductions include diversification of target species and to increase angler satisfaction with their catch-related experiences (Carpio et al. 2019; Hirsch et al. 2021). However, these introduced fishes often develop invasive populations, with biological invasions recognised as a major driver of biodiversity loss (Britton 2023). Given that fishes released for freshwater angling enhancement are generally large-bodied and of high trophic position then their invasive populations can have strong top-down effects that disrupt ecosystem functioning (Britton 2023).

Introductions of freshwater fishes for angling have resulted in a relatively small number of non-native fishes developing invasive populations globally, such as the North American largemouth bass *Micropterus salmoides* (Pereira and Vitule 2019). Ecological concerns on their invasive populations relate to the interactions with native prey fishes, where their increased predation pressure can lead to substantial

declines in prey population abundances (Gratwicke and Marshall 2001). Omnivorous species such as common carp *Cyprinus carpio* and goldfish *Carassius auratus* have been used to enhance recreational fisheries across much of Europe, with releases of both species being commonplace in many waters, despite high ecological concerns through middle-out effects (Britton et al. 2010).

Where introductions of multiple non-native species are released into novel communities that are taxonomically similar, such as carp and goldfish, then this raises additional concerns over their hybridisation, as this can alter the functional traits and ecological interactions of the hybridised progeny versus their parental species (Selz and Seehausen 2019). This results from the generation of novel phenotypes arising from the combining of alleles that have not segregated before in the same population (Selz and Seehausen 2019). Although hybridisation results in a general surge of genetic variation from the admixed divergent genomes and the acquisition of specific adaptive traits through lateral gene transfer and introgression (Seehausen 2004), its effects on ecological performance are unpredictable. For example, providing that the interactions between the alleles do not result in intrinsic incompatibilities then transgressive segregation can result in the hybrids outperforming parental taxa via adaptive diversification from the novel combination of parental traits and/ or expression of new traits (Kagawa and Takimoto 2018; Nieto Feliner et al. 2020). Conversely, introgression can result in the performance and fitness of hybrids being lower than their parental species through outbreeding depression (Pregler et al. 2023). In hybrids of the F1 generation, the general patterns tend to be an expression of high hybrid vigour through heterosis, where their expressed traits are superior in performance to those of their parents (Šimková et al. 2021; Dong et al. 2022). This is evident in the ecological impact observed in North America, where hybrids of the native Pecos pupfish (*Cyprinodon pecosensis*) and the invasive sheephead minnow (*Cyprinodon variegatus*) are ecologically superior to their parent species through higher growth rates and greater swimming endurance (Kodric-Brown and Rosenfield 2004). Additionally, research on hybrid forms of endemic and invasive *Barbus* spp. in European freshwater systems revealed these hybrids had larger body lengths for their age than pure endemic forms (De Santis et al. 2021). Moreover, the *Barbus* population with the largest trophic niche, had the highest number of introgressed alleles with invasive European barbel (De Santis et al. 2021).

Heterosis in the F1 generation is especially important to consider when the parental species are both high impacting non-native species of global concern, such as in carp and goldfish. Both species prefer waters of > 20 °C and are highly invasive globally with foraging behaviours that drive dietary overlaps with native fishes and strongly modify ecosystem functioning (Britton et al. 2010; Britton 2023). In recreational freshwater fisheries where these fishes co-exist, fertile hybrids are often produced (Hänfling et al. 2005). In the England and Wales, hybrids between these species are produced in hatcheries and are then frequently released into lentic catch-and-release fisheries to enhance angling performance. With England and Wales having a temperate climate with water temperatures only occasionally exceeding 20 °C (Amat Trigo et al. 2024) then the ecological performance of these fishes might be constrained in current conditions but accelerate as waters warm through climate change (Ruiz Navarro et al. 2016). Accordingly, testing the performance of these fishes across a temperature range enables their performances to be tested in varying thermal conditions that are ecologically relevant (Ferreira et al. 2014). Given that temperature is a key driver of metabolic rates in ectotherms, influencing their growth rates, feeding behaviour, and overall ecological performance, it is crucial to examine how these species

and their hybrids respond to temperatures that reflect both their thermal optima and potential environmental variations (Britton et al. 2010), especially with rising global temperatures altering the thermal landscape of aquatic ecosystems (Priya et al. 2023).

Comparative functional responses (CFR) and specific growth rates (SGR) can be used as proxies for ecological performance of invasive species and applied to forecasting the ecological effects of existing, emerging, and future invasive alien species (Dick et al. 2017; Britton et al. 2018). The functional response specifically examines the relationship between resource availability and consumer uptake (Holling 1959) and can, for example, estimate maximum consumption rates. This approach has proven particularly useful in deriving per capita impacts of invasive non-native species when used comparatively with trophically analogous native species (e.g., Alexander et al. 2014; Dickey et al. 2018). Specific growth rates (SGRs) can test the effect on body mass of how co-existing species compete for fixed food resources versus the species in allopatry, helping identify which species are the superior competitors and the effect of their resource acquisition at individual and group level (Britton 2018). Consequently, CFRs and SGRs provide highly complementary tools for assessing the outcomes of novel interactions of invasive fishes.

The aim here was thus to provide the evidence base for the risk analysis of hybrids arising from the introgression of genes between taxonomically similar species using carp and goldfish as model species to experimentally test their foraging behaviours (as CFRs) and growth performance (as SGRs) versus their first-generation (F1) hybrids in contexts of two contrasting temperatures. We predict that the ecological performance of the F1 fish will be superior to both non-hybrid carp and goldfish through higher consumption rates that provide superior competitive abilities when in sympatry with their parental species which results in faster growth rates, with this heterosis being independent of temperature.

Materials and methods

Experimental fish

The experimental carp, goldfish and F1 hybrids were from the same hatchery in Southern England, where the fish were produced from the same parental lines, and with experimental fish exposed to the identical rearing conditions. Both parental species have thermal optima > 20 °C and critical thermal maxima > 30 °C (Britton et al. 2010; Ferreira et al. 2014). All fish were age 0+ years and of initial body mass 2.0 to 6.0 g on arrival in the laboratory, where they were then individually tagged (7 mm passive integrated transponder tag), and acclimated for 20 days (18 °C; 16:8 h light: dark cycle). Outside of experiments, the fish were held in stock tanks (90 L, flow-through system; n = ~30 fish per tank, species held separately) and fed a maintenance diet of crushed pelletized fishmeal. As the initial CFR experiments were completed at 18 °C, the fish were initially held in their stock tanks at this temperature.

Comparative functional response experiments

For CFR experiments, individual fish were exposed to Chironomid larvae as prey resources in 10 L tanks at 18 °C following a 24-hour starvation period and a 4-hour acclimation period to their experimental tank. Food densities were 4, 8, 16, 32 and 64 larvae (and 128 for the 26 °C experiment). Food exposure was for

one hour, after which the number of larvae consumed was quantified, with three replicates per prey density per species. When all replicates were completed, the fish were returned to the stock tanks. The water temperatures of both the stock and experiment tanks were then increased to 26 °C over 8 days and, following a 5-day acclimation period, the CFR experimental process was repeated. With the fish being PIT tagged, no individual fish was used more than twice in CFRs, with a minimum of five days between use (with fish used randomly across the experiments).

Values of the CFR parameters attack rate (a) and handling time (h) were calculated for each species and temperature using maximum likelihood estimation (MLE) in the Random Predator Equation (Rogers 1972), completed in the R package '*Frair*' (Pritchard et al. 2017). The equation assumes a Type II functional response and the non-replacement of prey, where $N_e = N_0 (1 - \exp(a(N_e h - T)))$, with N_e = number of prey eaten, N_0 = initial density of prey, a = attack rate, h = handling time and T = total time. Analyses also provided the significance of differences in a and h between the species (Pritchard et al. 2017; Cuthbert et al. 2019). To visualise uncertainty, 2000 non-parametric bootstraps enabled empirical 95% confidence intervals to be fitted around the functional responses, which were used to provide CFR plots between the parental species/ F1s, and water temperature.

Specific growth rate experiments

Following completion of CFRs, all water temperatures were returned to 18 °C and the fish acclimated for 10 days in the stock tanks. The competitive growth performance of the fishes was then tested using SGRs through completion of co-habitation experiments completed in tanks of 25 L. Experimental treatments used controls (species/hybrid in allopatry; n = 6) and treatments (combinations of two species in sympatry; n = 3 + 3; and all species in sympatry; n = 2 + 2 + 2), each replicated three times. Each species per experimental treatment was batch weighed (to 0.01 g) before being released into their tanks, where they were held at 18 °C and fed a daily food ration (crushed pelletised fishmeal) at a mean of 2% starting body mass. After 15 days, the fish were removed from their tanks, re-weighed, returned to their tanks and the water temperature increased to 26 °C over five days before the experimental process was repeated. For each species/hybrid, control and treatment, and water temperature, SGR was determined from $([(\ln W_{t+1}) - \ln W_t) / {}_t]/n) \times 100$ (Equation 1), where W_t = total starting weight of the species in the tank, W_{t+1} = total finishing weight, n = number of fish, and ${}_t$ = number of days between W_t and W_{t+1}. A generalised linear model (GLM) tested the differences in SGR between treatments for each species, where SGR was the dependent variable, treatment was the independent variable, and total starting mass of fish per replicate used as an initial covariate and retained in final models when its effect was significant. Model outputs were the overall significance of the model and the mean SGR values (± 95% CI) according to species and treatment. All analyses were performed in R (version 4.2.3; R Core Team 2023).

Results

Comparative functional responses

The functional responses of all species at all temperatures were Type II and significant (Fig. 1; Suppl. material 1). The 95% confidence intervals of consumption

rates at 18 °C suggested carp had significantly higher rates than goldfish and hybrids, which had similar values to each other (Fig. 1). All species revealed higher consumption rates at 26 °C versus 18 °C, with no significant differences between them. Attack rates of carp and hybrids were also significantly higher at 26 °C versus 18 °C, but not for goldfish. For all species and the hybrids, handling times were lower at 26 °C than 18 °C (Table 1; Suppl. material 1). There were also significant differences in these metrics between the species at both temperatures, with the attack rate of carp being lower than the other fishes at both temperatures (Table 1).

Specific growth rates

Increased fish mass occurred in all SGR treatments at both temperatures (Fig. 2; Suppl. material 1). The effect of treatment on SGR was significant for each species (GLM: carp: Wald χ^2 = 452.39, *df* = 22, $p < 0.0001$; goldfish: Wald χ^2 = 130.91, *df* = 23, $p < 0.001$; hybrid: Wald χ^2 = 128.92, *df* = 22, $p = 0.002$), where starting mass as a covariate was significant for carp ($p = 0.01$) and hybrids ($p = 0.03$) (retained in

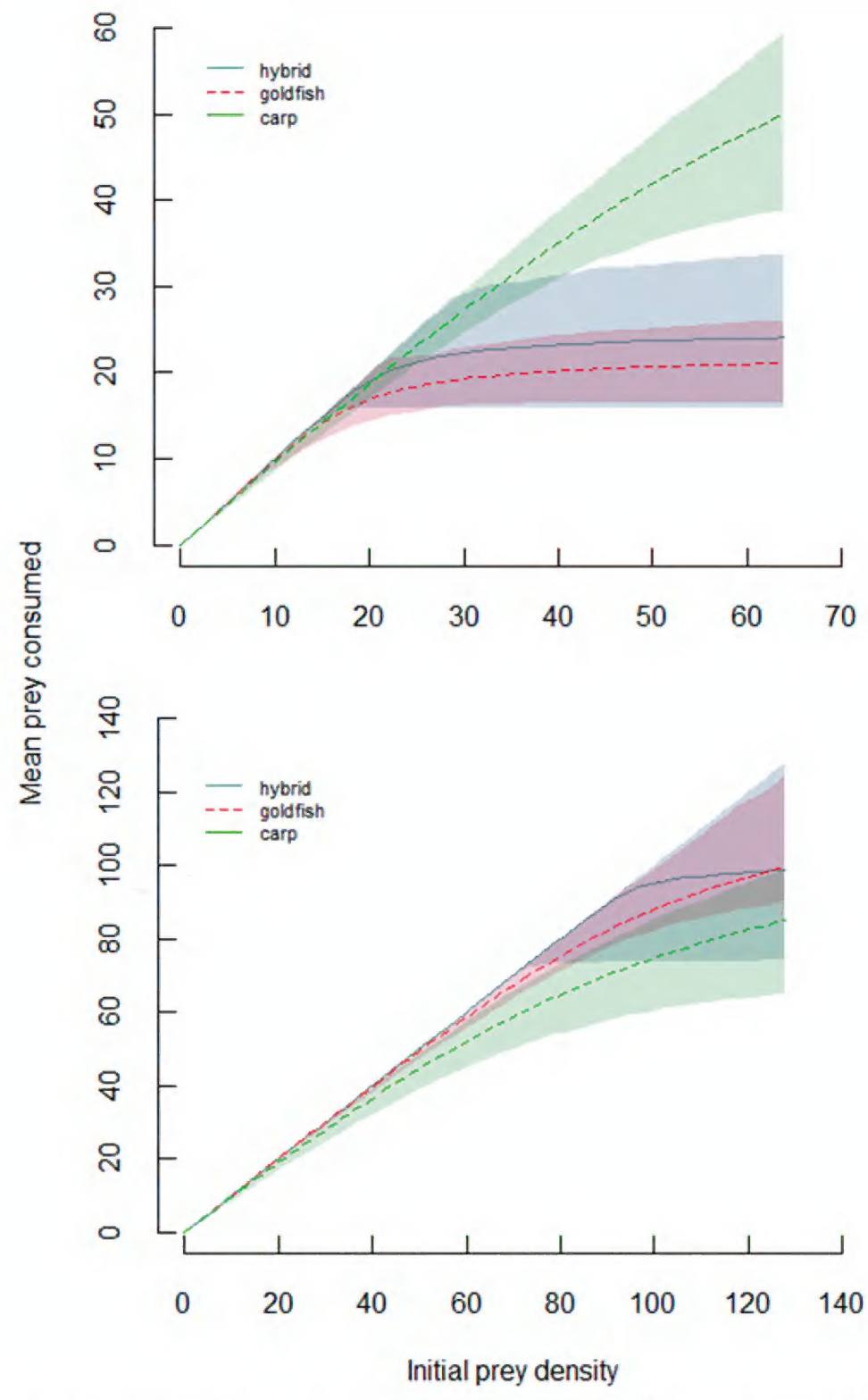

Figure 1. Comparative functional response curves for carp, goldfish and their F1 hybrids at 18 °C (top plot) and 26 °C (bottom plot). Shaded areas around the curves represent 95% confidence intervals generated by boot-strapping. Note differences in values on both axes between the plots. The mean prey consumed was over the period of 1 hour.

Table 1. First order linear coefficient results from logistic regressions for the predator and prey combinations (A). All values indicate a Type II functional response. Parameters of the comparative functional responses, with statistically significant differences in the parameters between species ($\alpha = 0.05$) in bold. a = attack rate, h = handling time (B). Z and P values are statistical outputs from regression that indicate whether a and h differ significantly between the comparator species.

(A)

Temperature	Species	Linear coefficient	P	Pseudo R^2
18 °C	F1	-0.09	<0.0001	0.63
	Goldfish	-0.06	<0.0001	0.67
	Carp	-0.03	0.0001	0.65
26 °C	F1	-0.06	0.001	0.69
	Goldfish	-0.04	<0.0001	0.70
	Carp	-0.02	<0.0001	0.68

(B)

18 °C	F1/Goldfish	F1/Carp	Goldfish/Carp
a	12.72/7.67	12.72/3.43	7.67/3.43
Z	-1.15	2.34	2.11
P	0.25	**0.02**	**0.04**
h	0.04/0.05	0.04/0.01	0.05/0.01
Z	1.10	8.11	8.77
P	0.27	**< 0.001**	**< 0.001**
Pseudo R^2	0.63/0.67	0.63/0.65	0.67/0.65
26 °C			
a	42.18/6.89	42.18/3.46	6.89/3.46
Z	-8.55e7	-19.59e7	3.28
P	**< 0.001**	**< 0.001**	**0.001**
h	0.010/0.008	0.010/0.008	0.008/0.008
Z	-3.39	-12.54	-0.19
P	**< 0.001**	**< 0.001**	0.87
Pseudo R^2	0.69/0.70	0.69/0.68	0.70/0.68

final models), but not goldfish ($p = 0.16$; removed from final model). At both temperatures and all species, SGRs in the allopatric controls were generally lower than in the sympatric treatments, but with the effect of temperature on SGR being minor; where elevated SGRs were apparent then this was at 18 °C rather than 26 °C (Fig. 2).

Discussion

There was no evidence to suggest heterosis was apparent in the performance of the F1 hybrids across both experiments, with their performance in CFRs being weak versus carp at 18 °C and differences in consumption rates not being significant at 26 °C. Their CFR metrics were significantly higher at the elevated water temperature, but this was also apparent in goldfish, with the maximum consumption rates of all of the fishes being similar at this elevated temperature. The SGR experiment also did not indicate any substantially enhanced performance in the F1 fish versus the other fishes, nor was there a strong effect of temperature on SGR, most likely due to the feed rations being maintained at a constant level across both temperatures.

Heterosis is a common outcome of hybridisation in early generations, as observed in invasive plants (Hahn and Rieseberg 2017), where admixture can increase performance across multiple generations (Li et al. 2018), and in fishes, where similar patterns of heterosis were detected in crosses of three-spine stickleback *Gasterosteus aculeatus* from different lake populations (Thompson and Schluter 2022).

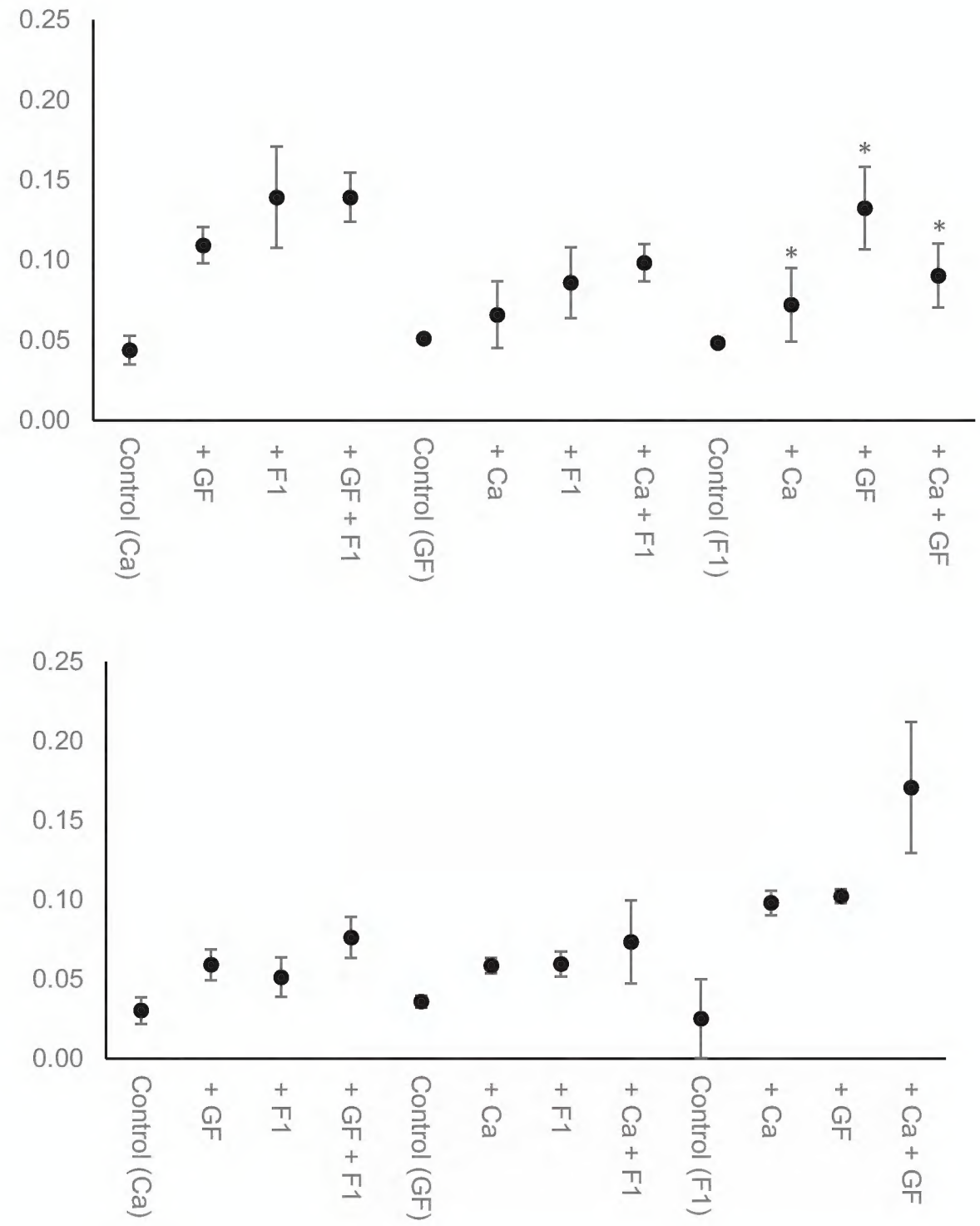

Figure 2. Mean specific growth rates of cohabitation experiments for carp ('Ca'), goldfish ('GF'), and their F1 hybrids ('F1') at 18 °C (upper) and 26 °C (lower). * denotes significant differences between treatments.

Interspecific hybridisation is common in freshwater fishes (Bolnick 2009), with the few performance studies on inter-specific hybridisation involving invasive fishes in the wild yielding equivocal results. For example, low larval mortality in the F1 generation of non-native red shiner *Cyprinella lutrensis* and native blacktail shiner *Cyprinella venusta stigmatura* was suggested as evidence of heterosis (Blum et al. 2010). However, in early generation hybrids of Asian bighead carp species (*Hypophthalmichthys* spp.), nutritional performance was intermediate between the parental lines, with advanced generations then becoming increasingly similar to parental species (Liss et al. 2016). However, hybrids of *Barbus* spp. were larger and had larger trophic niches than endemic parent species (De Santis et al. 2021). Heterosis in the performance of F1 generations of fishes mixed in aquaculture is more evident (Šimková et al. 2022) where advantages can include decreased viral susceptibility and faster growth rates (Bryden et al. 2004).

Our results, generated using hybrids and parental species under controlled conditions, represent novel outcomes as we could find no similar studies comparing the ecological performance of such high-impact invasive species versus their F1 generation. Although we concluded that F1 hybrids were not more impactful than their parental species, this should not be interpreted as an indication that they pose

no management concern. On the contrary, our findings suggest that F1 hybrids are equally impactful, which implies that they should be managed with the same level of concern as the parental species. Furthermore, while only F1 hybrids were tested in this study, it is important to recognise that advanced generations of hybrids can exhibit increased similarities to the parental species, as seen in other studies (Hänfling et al. 2005; Liss et al. 2016). This highlights the necessity of considering the potential ecological impacts of these advanced generations in future research and management strategies. Therefore, our study provides critical insights into the ecological performance of F1 hybrids, but with further investigation needed into the long-term ecological impacts of hybridisation, where there is a need to better understand the behaviour of later-generation hybrids.

This absence of transgressive segregation and heterosis in the hybrids of these globally invasive fishes is then important for their risk screening within management frameworks regulating the release of non-native fishes in recreational fisheries (Vilizzi et al. 2019; Copp et al. 2021). Both parental species have been assessed in risk screening as being of high ecological risk where, for example, they were assessed as representing the highest ecological risk of all non-native fishes introduced into freshwaters in England (Britton et al. 2010). Consequently, there was high concern that their hybrids would be composed of novel phenotypes that result from combinations of alleles that were previously always segregated (Selz and Seehausen 2019). Given there was no evidence that the F1 generation had superior performance in their foraging and growth rate, especially at 18 °C where carp were superior, but also at 26 °C where differences between the species were generally not significant, then this represents an important outcome for their scientifically informed management. Accordingly, the ecological concerns with introductions of these species remain with their parental populations and so where risk-based invasion management programmes are implemented to minimise the impact and dispersal of these species, they do not need to account for the possibility of these species producing hybrids that will accelerate their ecological impacts. This means that where invasive populations develop from fishes initially introduced for recreational angling then control and containment programmes could be effective in reducing the impacts of their populations (Britton et al. 2023), with the evidence base for such management decisions enhanced by the results presented here.

These results are particularly relevant in the context of climate change, which is expected to increase water temperatures globally (Britton et al. 2010; Ruiz Navarro et al. 2016). The lack of significant differences in performance between the hybrids and parental species at 26 °C suggests that, under warmer conditions, the hybrids do not exhibit superior ecological performance. This is an important consideration as rising temperatures might otherwise be expected to exacerbate the impacts of invasive species (Fobert et al. 2013), including their hybrid forms. The similar performance across species at elevated temperatures indicates that while these fishes can thrive in warmer conditions, the hybrids do not pose an increased threat beyond that already posed by the parental species. This finding contributes to our understanding of how these species might behave under future climate scenarios, where water temperatures in many regions may exceed the current norms (Emiroğlu et al. 2023). Furthermore, the co-habitation treatments in this study allowed for an assessment of how these species interact when placed in shared environments. The absence of significant differences in performance between the hybrids and their parental species during co-habitation suggests that the hybrids do not pos-

sess competitive advantages that would allow them to outcompete their parental species in shared habitats (but see Kodric-Brown and Rosenfield 2004; De Santis et al. 2021). This finding is important for understanding potential interactions in the wild, where these species might co-occur. However, it is important to note that while these findings are significant for the species studied (carp and goldfish), they may not necessarily generalise to other fish species. The specific ecological and genetic contexts of different species combinations could lead to different outcomes, and caution should be exercised before applying these results to other cases.

It is also important to acknowledge the limitations of this study. One limitation is that only the F1 generation was examined, and the long-term ecological impacts of advanced generations of hybrids were not assessed. As other studies have shown, advanced generations of hybrids can exhibit increased similarities to parental species, potentially leading to different ecological outcomes (Liss et al. 2016). Additionally, the controlled conditions of the experiments may not fully replicate the complexities of natural ecosystems, where factors such as predation, competition, and varying resource availability could influence the performance of these species and their hybrids.

Future research should focus on evaluating the performance of advanced hybrid generations under a wider range of environmental conditions, including varying temperatures and more complex ecological interactions. It would also be valuable to investigate the potential for hybrid vigour or outbreeding depression in these later generations, which could have significant implications for their ecological impact. Moreover, field studies that examine the behaviour and performance of hybrids and parental species in natural settings would help to validate and extend the findings from this controlled study.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Funding

No funding was reported.

Author contributions

JRB conceived the study and experimental design. AST and IK collected data. All authors analysed data, and drafted and edited the manuscript, and agree to be held accountable for the work performed therein.

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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Supplementary material 1

Raw data for functional response and specific growth rate

Authors: Ali Serhan Tarkan, Irmak Kurtul, J. Robert Britton

Data type: xlsx

Explanation note: All raw data collected through experiments in the study.

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Link: https://doi.org/10.3897/neobiota.95.126656.suppl1